Comparison of four methods of grassland productivity assessment based on *Festuca pallescens* phytomass data

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Abstract

The relative utility of 4 methods for grasslands above-ground net primary productivity (ANPP) assessment were evaluated. These methods, applied to a set of phytomass and litter data collected at about bimonthly intervals for 2 years in a *Festuca pallescens* (St. Yves) Parodi grassland steppe of southwestern Chubut, Argentina, were: (1) summation of positive increments of green (live) biomass between harvests, (2) summation of positive increments of total phytomass between harvests, (3) summation of positive increments of green biomass between harvests plus correction factors which accounted for the concomitant increases in dry, old dead, and litter, respectively, and (4) mathematical model of simultaneous differential equations which fitted the values of phytomass data obtained in the field. Method 1 gave consistently ($p \leq 0.05$) the lowest ANPP values in both years. Productivity values obtained with methods 2, 3, and 4 were highly correlated and did not differ significantly ($p \leq 0.05$) with each other. Their estimates varied from 94.8 to 105.3 g of dry matter per m^2 for the first year and from 73.0 to 149.4 g of dry matter per m^2 for the second year. These values are within the range of productivity given for other climatologically and physiognomically similar semiarid grasslands of North America. Each method except 1 provided reliable estimations of ANPP for the grassland studied. Methods 2, 3, and 4 can also be used to assess ANPP in any other grassland with similar characteristics. Each one, however, might have particular applications according to the specific objectives pursued.

Key Words: ***Festuca pallescens*, dynamic model, Patagonia**

Aboveground net primary production (ANPP), defined as the biomass per unit of time which is incorporated into the aerial parts of the plant community, is one of the parameters of most value for rational range development planning (Le Houérou et al. 1988).

While the concept of ANPP is simple to define, its measurement is not so simple, especially when dealing with natural grasslands. In these ecosystems, several methods have been proposed for ANPP estimation. These methods varied from indirect nondestructive techniques based on gas exchange techniques (Billings et al. 1966, Bingham et al. 1980), allometric equations (Johnson et al. 1988), and capacitance meter (Currie et al. 1987), to the direct and more generalized which involve periodic harvest of phytomass (Krishnamurthy 1979).

During the last decade, several studies focused on the rationale behind different methods for grassland ANPP estimation based on series of phytomass data (Kennedy 1972, Lauenroth 1973, Kelly et al. 1974, Singh and Yadava 1974, Singh et al. 1975, Krishnamurthy 1979). These studies showed that different methods of calculation applied to the same set of phytomass data generally produce ANPP values which are highly correlated with each other, although they may yield significantly different ANPP estimates. These studies also showed that since there is no procedure available to obtain the true ANPP value for comparison, each method may have its merits and demerits according to the type of vegetation sampled and the particular objectives pursued.

In the Argentine Patagonia, herbage yield and carrying capacity of different rangeland areas have been estimated mainly based on empirical observations. Rangeland deterioration caused by overgrazing appeals for a more rational setting of stocking rates, for which the knowledge of reliable estimations of ANPP is of fundamental interest.

The objective of this study was to compare 4 methods of assessing ANPP of a grassland steppe of *Festuca pallescens* (St. Yves) Parodi, to determine their relative utility based on theoretical and utilitarian considerations.

Methods

Study Area

Phytomass data were obtained from an area that was excluded to grazing in 1981 at Media Luna Ranch (45° 36′ S, 71° 25′ W) in the province of Chubut, Argentina. This area, representative of the sub-Andean Floristic District of the Patagonian Phytogeographic Province (Soriano 1956), is a homogeneous grassland steppe widely dominated by the tussock grass *F. pallescens*. This species, a typical cool-season grass which maintains active tillers the entire year, is one of the best Patagonian forage grasses because of its palatability and preference by sheep (Boelcke 1957, Parodi 1959).

The climate of the area is semiarid, cold in winter and warm in summer with the growing season extending from September through April. Mean annual temperature is 4.5° C, and warmest month is January (mean temperature 11.7° C) and the coldest July (mean temperature −3.7° C). Annual rainfall averages 374 mm, 67% of which occurs in fall and winter in the form of either rain or snow. Soils are sandy-loam, fine gravelly on the surface and stony below (Xerorthents) (Beeskow et al. 1987).

Data Collection

We used a set of aerial phytomass and litter data collected within the exclosure at about monthly or bimonthly intervals for 2 years (fall 1981 to fall 1983) to comprise 2 full growing seasons. Fifteen circular plots 1 m in diameter were randomly located within the exclosure at every sampling date. The phytomass inside each plot was harvested to ground level and litter collected. The number, size, and shape of the plots used produced phytomass data of *F. pallescens* within 10% of error of the mean at the 5% probability level according to Milner and Hughes' (1970) formula. Phytomass was separated by species into green, dry, old dead, and litter components (Defossé et al. 1990), ovendried at 70° C to constant weight, and weighed. From this set, and for practical purposes of calculation of this study, we only used data of *F. pallescens,* since this species comprised more than 95% of all phytomass sampled throughout the study period.

Methods of ANPP Calculation

(1) Summation of positive increments of green phytomass between harvests (Krishnamurthy 1979), hereafter method 1; (2) summation of positive increments of total phytomass between harvests (Singh et al. 1975), hereafter method 2; (3) summation of positive increments of green phytomass plus correction factors which accounted for the concomitant increases in dry, old dead, and litter, respectively, hereafter method 3. The estimated annual

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ANPP with this method is: ANPP = $\sum_{i=1}^{n}$ Gc + Dc + Odc + Lc where:

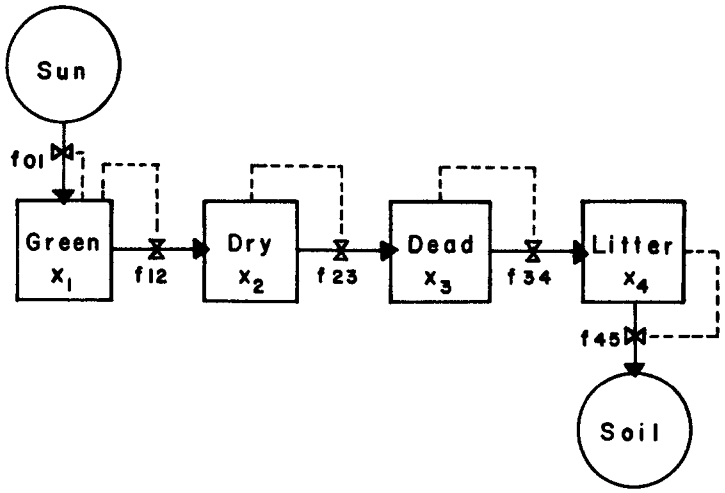
$$\begin{aligned}
Gc &= \Delta^+ \text{Green} / t2 - t1 \text{ (if the value is negative, is called S)} \\
Dc &= (\Delta^+ \text{Dry} / t2 - t1) - \text{S} \quad ; (Dc \geq 0) \\
Odc &= (\Delta^+ \text{Old Dead} / t2 - t1) - \Delta^- Dc \quad ; (Odc \geq 0) \\
Lc &= (\Delta^+ \text{litter} / t2 - t1) - \Delta^- Odc \quad ; (Lc \geq 0)
\end{aligned}$$

This method accounts for the phytomass transfer between components during each sampling interval (t_2–t_1), and at the same time avoids any double addition (Krishnamurthy 1979). It is conceptually similar to the method used by Sala et al. (1981) to estimate ANPP of a temperate grassland. The constraint used for methods 1, 2, and 3 was that for each phytomass component the increments were added only if mean values were significantly different ($p<0.05$) from one period to the next. Differences in mean values of each phytomass component were analyzed by an ANOVA and mean separation was by Fisher's LSD procedure (Ott 1984). The last method, hereafter method 4, is a mathematical model of simultaneous differential equations with time variable coefficients between intervals (Fig. 1), which fitted mean phytomass values obtained in the field plus or minus the confidence interval at $p<0.05$ (Ares 1978, Bertiller 1984). Mean phytomass values of green dry, old dead, and litter obtained during the first sampling date are thus introduced in the model as the initial values. The time variable coefficients f_{ij}, which represent relative rates of the processes of productivity, senescence, death, and decomposition are estimated by iteration until the calculated phytomass values fit those obtained in the subsequent sampling dates ($\pm$ confidence interval at $p<0.05$). These coefficients are assumed to be constant between 2 sampling dates. With this method, daily ANPP is estimated as:

$$\text{ANPP } (g\ m^{-2}\ day^{-1}) = f_{01}\ (g\ g^{-1}\ day^{-1})\ X_1\ (g\ m^{-2}).$$

The model assumes that during a specific time interval, at least one of these processes (productivity, senescence, death, or decomposition) does not occur simultaneously with each other, and thus is taken as 0. The decision of which coefficient is taken as 0 during a specific time interval is based on biological rationale by inspecting the biomass slopes of all components during that time interval (Bertiller 1984).

Relationships among estimates obtained with the 4 methods were investigated by correlation and simple regression analyses



$$\begin{aligned}
\dot{X}_{1,t} &= X_{1,t} \cdot f_{01} - X_{1,t} \cdot f_{12} & X_{1(t+1)} &= \dot{X}_{1(t)} \cdot \Delta t + X_{1(t)} \\
\dot{X}_{2,t} &= X_{1,t} \cdot f_{12} - X_{2,t} \cdot f_{23} & X_{2(t+1)} &= \dot{X}_{2(t)} \cdot \Delta_t + X_{2(t)} \\
\dot{X}_{3,t} &= X_{2,t} \cdot f_{23} - X_{3,t} \cdot f_{34} & X_{3(t+1)} &= \dot{X}_{3(t)} \cdot \Delta_t + X_{3(t)} \\
\dot{X}_{4,t} &= X_{3,t} \cdot f_{34} - X_{4,t} \cdot f_{45} & X_{4(t+1)} &= \dot{X}_{4(t)} \cdot \Delta_t + X_{4(t)} \\
\dot{X}_{5,t} &= X_{4,t} \cdot f_{45}
\end{aligned}$$

$\dot{X}_{n,t}$ = first order time derivative $(g.m^{-2}.\ day^{-1})$

$X_{n,t}$ = state variables $(g\ .\ m^{-2})$

f_{ij} = time variable specific activity coefficients $(g.g^{-1}.day^{-1})$

Fig. 1. Diagram showing the energy flow in the grassland of *Festuca pallescens* in Patagonia (Top). Boxes represent state variables, circles represent the energy source (Sun) and sink (soil). Arrows are flows (solid lines) or control of flows (dashed lines).
Linear homogeneous differential equations (bottom) of the compartment model used to compute ANPP from Green (X_1), Dry (X_2), Old dead (X_3), and Litter (X_4) according to Ares (1978) and Bertiller (1984).

Table 1. Above-ground net primary productivity (ANPP) values obtained by applying different methods[1] to the same set of *Festuca pallescens* phytomass data (in g m^{-2} period^{-1}).

Season		Growth Period		(Days)	Method 1	Method 2	Method 3	Method 4
		(Date)	(Date)	(Days)	----	(g m^{-2} period^{-1})	----	
fall	1	22 May	to 12 Aug.	82	0.0	0.0	0.0	0.0
winter	2	12 Aug.	to 17 Sept.	36	0.0	0.0	0.0	3.0
spring	3	17 Sept.	to 21 Oct.	34	7.2	0.0	7.2	7.4
spring	4	21 Oct.	to 2 Dec.	42	8.2	20.2	8.2	8.3
spring/summer	5	2 Dec.	to 15 Jan.	44	0.0	23.4	28.2	32.7
summer	6	15 Jan.	to 18 Mar.	61	0.0	55.8	51.2	53.9
		Total		300	15.4	99.4	94.8	105.3
fall/winter	7	18 Mar.	to 10 Aug.	146	0.0	0.0	0.0	0.0
winter/spring	8	10 Aug.	to 29 Sept.	50	7.5	0.0	40.6	7.4
spring	9	29 Sept.	to 9 Nov.	41	12.4	0.0	12.3	12.8
spring	10	9 Nov.	to 21 Dec.	42	0.0	0.0	0.0	0.0
summer	11	21 Dec.	to 9 Feb.	43	0.0	0.0	28.3	16.2
summer	12	9 Feb.	to 21 Mar.	47	9.7	73.0	68.2	44.3
		Total		369	29.6	73.0	149.4	80.7

[1]Methods are:
1 = Summation of positive increments of green phytomass between harvests
2 = Summation of positive increments of total phytomass between harvests
3 = Summation of positive increments of green phytomass plus correction factors which accounted for the concomitant increases in dry, old dead, and litter, respectively.
4 = Mathematical model of simultaneous differential equations with time variable coefficients.

(Sokal and Rohlf 1981).

Results and Discussion

Above-ground net primary productivity values per sampling period, estimated with the 4 different methods, are shown in Table 1. The values for the first year (300 days) ranged from 15.4 g of dry matter per m^2 with method 1 to 105.3 g of dry matter per m^2 with method 4. Aerial productivity for the 369-day period of the second year ranged from 29.6 g of dry matter per m^2 with method 1 to 149.4 g of dry matter per m^2 with method 3. Method 1 consistently produced the lowest values of ANPP accumulated, representing only 15 and 20% of the maximum estimate for the first and second year, respectively. Methods 2, 3, and 4 produced ANPP estimates which are highly correlated and do not significantly differ ($p<0.05$) from each other, whereas method 1 was poorly correlated with the other 3 methods and yielded significantly different ($p<0.05$) estimates (Table 2). Considering the ANPP per sampling period, similar values were computed by methods 1, 3, and 4 during early and mid-spring, when senescence rates of *F. pallescens* are very low (Bertiller and Defossé 1990). Method 1, however, failed in detecting the productivity that occurred during mid-summer, when senescence rates of this species are very high (Bertiller and Defossé 1990). Since method 1 did not account for the senescence process, it underestimates the real ANPP of this grassland during mid-summer. This is in agreement with several studies (Lauenroth 1970, Milner and Hughes 1970, Singh and Yadava 1974), which pointed out that the consideration of live component only may lead to serious underestimates of ANPP. Singh et al. (1975) arrived at the same conclusion by applying method 1 to phytomass data of several semiarid grasslands of North America. This method, thus, should be discarded for ANPP estimation in either this or any other grassland with similar phenological and climatological characteristics.

Table 2. Simple correlation matrix coefficients comparing the 4 methods.[1]

Method	1	2	3	4
1	1.00	0.18*	0.26*	0.07*
2		1.00	0.81	0.89
3			1.00	0.85
4				1.00

[1]Methods are:
1 = Summation of positive increments of green phytomass between harvests
2 = Summation of positive increments of total phytomass between harvests
3 = Summation of positive increments of green phytomass plus correction factors which accounted for the concomitant increases in dry, old dead, and litter, respectively.
4 = Mathematical model of simultaneous differential equations with time variable coefficients.
*Significantly different at $p\leq0.05$.

Considering the daily rates of ANPP (in g m^{-2} day^{-1}) the highest values were recorded in late summer by the methods which included the senescence process (2, 3, and 4), whereas method 1 presented them in spring (Table 3).

Although *F. pallescens* lacks dormant periods and shows some active tillers during winter (Soriano 1956, Defossé et al. 1990) no productivity was detected by any method from late summer to late winter. In early spring of the second year a high value of productivity was computed by method 3. This high estimate was caused by an unusual increase observed in mean values of litter, which weighed more than any other component in the estimation of ANPP during this period. Litter has also been considered the most difficult component to utilize in ANPP calculations because of its variability (Singh et al. 1975), and this was corroborated in our study. While the coefficients of variability (C.V.) of green, dry, and old dead components ranged from 8 to 14%, C.V. of litter varied from 13 to 24% at all sampling dates.

The values obtained with methods 2, 3, and 4 are within the range of above-ground productivity given for other semiarid grasslands of North America with similar climatic and physiognomic characteristics. In a native grassland of Montana with 313 mm of annual precipitation and of a mean annual temperature 5.3° C. Black (1968), for example, reported ANPP of 122 g m^{-2} year^{-1}. Redman (1975) estimated ANPP of a grassland of western North Dakota with 350 mm of annual precipitation and 4.8° C mean temperature as 144 g m^{-2} year^{-1}. In Sundance, Wyoming, USA, Cosper et al. (1967) estimated an ANPP of 76 gm^{-2} year^{-1} for an area with 380 mm annual rainfall and 6.8° C mean annual temperature. Redente et al. (1988) estimated ANPP of a native grassland in Wyoming as 118 g m^{-2} year^{-1} using a procedure similar to our method 3. It is assumed that methods 2, 3, and 4 produced reliable ANPP estimates for the grassland studied.

Table 3. Daily values of above-ground net primary productivity (in g m^{-2} day^{-1}). Periods 1 to 6 represent the first year, while periods 7 to 12 the second year.

Season	Growth Period	(Date)	(Date)	(Days)	Method 1	Method 2	Method 3	Method 4
					(g m^{-2} period^{-1})			
fall	1	22 May	to 12 Aug.	82	0.00	0.00	0.00	0.00
winter	2	12 Aug.	to 17 Sept.	36	0.07	0.00	0.07	0.08
spring	3	17 Sept.	to 21 Oct.	34	0.21	0.00	0.22	0.22
spring	4	21 Oct.	to 2 Dec.	42	0.19	0.48	0.19	0.19
spring/summer	5	2 Dec.	to 15 Jan.	44	0.00	0.53	0.64	0.74
summer	6	15 Jan.	to 18 Mar.	61	0.00	0.91	0.96	0.89
fall/winter	7	18 Mar.	to 10 Aug.	146	0.00	0.00	0.00	0.00
winter/spring	8	10 Aug.	to 29 Sept.	50	0.15	0.00	0.81	0.15
spring	9	29 Sept.	to 9 Nov.	41	0.30	0.00	0.30	0.31
spring	10	9 Nov.	to 21 Dec.	42	0.00	0.00	0.00	0.00
summer	11	21 Dec.	to 9 Feb.	43	0.00	0.00	0.34	0.38
summer	12	9 Feb.	to 21 Mar.	47	0.21	1.55	1.47	0.94

[1]Methods are:
1 = Summation of positive increments of green phytomass between harvests
2 = Summation of positive increments of total phytomass between harvests
3 = Summation of positive increments of green phytomass plus correction factors which accounted for the concomitant increases in dry, old dead, and litter, respectively.
4 = Mathematical model of simultaneous differential equations with time variable coefficients.

Excluding method 1 for the reasons above mentioned, and from an utilitarian point of view in which no specific values per period are needed, method 2 seems to be a good choice. It requires less effort than methods 3 and 4 because it does not require phytomass separation into components, although it seems less precise in ANPP estimation per sampling interval. This method seems to be useful when a large number of plots needs to be sampled or different sets of data for a big area need to be evaluated. Methods 3 and 4 seemed to be the most reliable for ANPP assessment from a theoretical point of view, since the inclusion of different phytomass components in ANPP estimation allows for minimal loss of information. This gain in information should be balanced, however, against higher labor costs. The model (method 4) seems to be more precise in ANPP estimation than method 3, which is based only on mathematical manipulation of the phytomass data. The major advantage of the model resides in its flexibility to allow for external manipulations, which can include the simulation of the action of herbivores with different stocking rates, etc. Having animal consumption and preference data available, for example, a subtractive term can be easily incorporated into the first equation of the model. This will permit more precise setting of stocking rates than those based on both empirical observations or mathematical manipulation of the data (Ares 1978). With a similarly constructed model, for example, Turner (1988) simulated the carbon flow of a *Spartina alterniflora* Loisel. marsh, and used it to estimate an acceptable population size of feral horses.

In this paper we compared 4 methods for grassland ANPP estimation based on *F. pallescens* phytomass data. While method 1 underestimated the productivity of the range, the other 3 methods produced reliable ANPP estimations for the grassland studied. According to the objectives pursued, any of these may be successfully used to obtain reliable estimations of the production of different grassland areas of Patagonia or elsewhere, providing either 1 species is dominant or several grass species have similar phenology.

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